HABITAT PREFERENCES OF POLAR BEARS IN THE HUDSON BAY LOWLANDS DURING LATE SUMMER AND FALL

DOUGLAS A. CLARK,[1] Department of Biological Sciences, University of Alberta. Edmonton, AB T6G 2E9, Canada
IAN STIRLING, Canadian Wildlife Service, 5320 122 Street, Edmonton, ABT6H 3S5 Canada, email: ian.stirling@ec.gc.ca

Abstract: From late July through early November, polar bears (*Ursus maritimus*) in western Hudson Bay are on shore because the annual ice melts. During this period, bears segregate by age and sex classes into different habitats. We investigated habitat selection using the locations of 1,131 captures made from 1966 to 1994. Adult males, the most dominant bears, were found most often in coastal areas, especially on beach ridges. This enables them to keep cool during summer and move little while fasting until freeze-up, thereby conserving stored energy reserves. Lone adult females and females accompanied by dependent young moved inland during the ice-free period and selected riparian, lakeshore, and lichen tundra habitats. We conclude that avoiding adult males, thermoregulation, and suitable denning habitat are the most important factors causing adult females to move to the inland areas and to select habitats once there. Subadult females were distributed through all habitat types while subadult male distribution paralleled adult males. Production of berries, as a potential food source, probably does not influence inland distribution.

***Ursus* 10:243–250**

Key words: age and sex class, habitat, Hudson Bay Lowlands, polar bear, *Ursus maritimus*.

The polar bear population that inhabits western Hudson Bay spends the period from late July through early November on shore because the annual ice melts completely (Stirling et al. 1977). They cannot hunt seals during this period, and little feeding occurs on shore (Russell 1975, Knudsen 1978, Lunn and Stirling 1985, Ramsay and Hobson 1991, Derocher et al. 1993). In general, adult males remain on the coast, pregnant females and family groups move inland, and subadults of both sexes are found throughout the area (Stirling et al. 1977, Derocher and Stirling 1990*a*). Lone, apparently non-pregnant, adult females remain near the coast (Derocher and Stirling 1990*a*). Pregnant females dig earth dens in the inland areas and remain in or near them during late summer and fall (Jonkel et al. 1972). Pregnant females face greater energetic demands than bears of other age and sex classes because they fast for a total of about 8 months. When the rest of the population returns to the sea ice in early to mid-November, pregnant females remain ashore in dens to have and nurse cubs until about the following March, when they, too, return to hunting seals (Stirling et al. 1977).

The different distributions of bears of each age and sex class, relative to specific habitat types in coastal or inland areas, suggests that a variety of factors may be involved. For example, if simply being inactive to conserve energy was the only important factor, one would predict that all bears, except possibly pregnant females (which seek suitable denning sites in inland areas), would simply remain on the coast until freezeup. However, as a group, only adult male bears do so. In this paper, we examine the distribution of bears by age and sex class in relation to the habitats they occupy during the ice-free period and evaluate hypotheses, which may not be mutually exclusive, to explain the results.

We thank D. Andriashek, S.A. Boutin, W. Calvert, A.E. Derocher, N.J. Lunn, S. Miller, J.O. Murie, and P.A. Scott for assistance in the field, lab, and review of the manuscript. W. Calvert extracted the data on capture locations of bears of each age and sex class from the National Polar Bear Data Base. M.A. Ramsay provided access to data on bears handled during the course of his research. S. Barry gave valuable advice and assistance with the statistics. Financial and logistic support were provided by the Canadian Wildlife Service, the Zoology Department of the University of Alberta, the Canadian Circumpolar Institute (Northern Scientific Training Program), the Manitoba Department of Natural Resources, the Churchill Northern Studies Centre and the Natural Sciences and Engineering Research Council (operating grant to I. Stirling).

METHODS

Study Area

Our study area is on the western coast of Hudson Bay near Churchill, Manitoba from latitude 57°00'N – 58°50'N and from longitude 92°40'W – 94°00'W. The

[1]Present address: 150 Barkley Terrace, Victoria, BC V8S 2J6 Canada, email: doug_clark@pch.gc.ca

entire area is <200 m elevation and has little relief. It contains numerous lakes, rivers, and creeks and lies atop continuous permafrost. This region is a transition zone between boreal forest and low arctic tundra (Ritchie 1962).

Sampling of Polar Bears in Relation to Habitat

Polar bears on land were captured non-selectively each fall (late August to early November) from 1966 through 1994. Each bear was chemically immobilized using standard protocols, and all bears were individually marked, measured, and sampled (Stirling et al. 1989). The habitat a bear was in when first sighted was recorded.

For this study, we subjectively defined 12 habitats relative to their availability to polar bears. These definitions are based on the descriptions by Shelford and Twomey (1941), Sjörs (1959), Ritchie (1962), Kershaw (1976), Zoltai and Tarnocai (1975), Pierce and Kershaw (1974, 1977), Zoltai et al. (1988), Dredge and Nixon (1992), Clark (1996), and our unpublished observations.

High Availability.—

1. Lichen tundra—extensive, flat, treeless, inland areas dominated by lichen-covered polygonal peat plateaus, peat hummocks with *Ledum groenlandicum* (Labrador tea), *Rubus chamaemorus* (cloudberry), *Empetrum nigrum* (crowberry), and *Vaccinium* spp. (blueberry) in the depressions;
2. Coastal tundra—flat, treeless expanses, sometimes up to about 10 km inland from the coast, includes old raised beaches, patches of bare substrate widespread, vegetation dominated by *Dryas integrifolia* (avens), *Salix reticulata* (net-leaved willow), and *Arctostaphylos* spp. (bearberry);
3. Wetland—extensive throughout study area, includes fens and sedge meadows, sometimes with low densities of *Larix laricina* (larch);
4. Spruce forest—open spruce woodlands, mainly *Picea mariana* (black spruce) but also *P. glauca* (white spruce), along river drainages and on peat alluvial deposits;
5. Lakeshore—predominantly the shorelines of thermokarst lakes sometimes with no trees but more often with a fringe of *P. mariana* and occasional *Larix laricina* along the top of the bank which thins away from the edge before yielding to lichen tundra, various low bushes and wetland vegetation on lower banks and flats leading to water, including *Empetrum nigrum*, and *Vaccinium* spp.;

Medium Availability.—

1. Riparian—the edges of streams and rivers, with vegetation similar to lakeshore habitat;
2. Tide flat—unvegetated intertidal sand and mud flats parallel to the coast, up to several km wide at low tide;
3. Willow—thick patches of *Salix* spp. several meters across and sometimes continuous for several hundred meters between parallel beach ridges or along the edges of lakes in both coastal and inland areas;
4. Beach ridge—deposits of gravel and sand, elevated up to 5 m above the high tide line, parallel to shoreline, up to several km long, often vegetated with *Elymus arenarius* (sea lyme grass);

Low Availability.—

1. Hummock—dry mounds of peat in wetter areas, usually only a few meters in diameter, can be bare or partially vegetated with *Salix* spp. or *Picea mariana*;
2. Burn—areas of spruce forest or lichen tundra in various stages of post-fire succession.

Some observations were unclassified.

We summarized the number of bears of each age and sex class captured in each habitat from 15 August to 15 October, when they were most likely to be in whatever habitat they preferred during the period they were on land. Bears caught before or after those dates were excluded to minimize bias caused by capture of animals as they moved through a variety of habitats on route to inland sites shortly after leaving the ice or returning to the coast just prior to freeze-up. To reduce possible bias resulting from bears seeking human food and garbage near the town of Churchill, captures north of 58°44'N and east of 94°00'W were excluded. The categories of bears we analyzed in relation to habitat types were as follows: adult males, lone (usually pregnant) adult females, adult females with cubs-of-the-year (COY), adult females with yearlings, subadult males, and subadult females. We selected the most recent 200 records, starting in 1994 and going backward chronologically. If there were fewer than 200 records for an age or sex class of bears, we used them all. We chose 200 because that was an adequate sample for our purposes and was close to the number of records for age and sex groups for which we did not have 200 records.

We tested for independence by calculating a *G*-value with a likelihood-ratio test, using the frequencies of oc-

currence of each of the 6 age and sex classes in each of the 12 habitat types. To determine and display visually the relative strengths of associations between age and sex classes and habitat types, we applied 2-dimensional correspondence analysis to calculate eigenvalues, proportions of inertia accounted for, and a 2-dimensional plot of the relationships (Dixon 1992).

RESULTS

The number of polar bears of each age and sex class captured in each habitat type are presented in Table 1. The observed frequencies of occurrence of bears from each age and sex class in different habitat types varied significantly from the values expected, had there been no preferences (G = 410.3, 55 df, $P < 0.01$). About two-thirds of the contribution to the high G-value in the test for independence was made by a small number of habitats that appeared to be either selected for, or avoided by, specific age and sex classes of bears. In particular, adult males were found most often in coastal areas, especially on beach ridges: 79 of 200 (39.5%) were captured on beach ridges, 8 of 200 (4.0%) each on coastal tundra and tide flats, and 25 of 200 (12.5%) in willow thickets for a total of 120 of 200 (60%). Lone females were found mainly in riparian habitat (63 of 200; 31.5%) and lakeshores (57 of 200; 28.5%) which border lichen tundra more than tundra itself (33 of 200; 16.5%). Females with cubs-of-the-year (COYs) selected riparian strips (40 of 200; 20.0%), lakeshores (37 of 200; 18.5%), and lichen tundra (59 of 200; 30%). Females with yearling cubs showed a similar distribution to females with COYs (Table 1): 38 of 149 (26%) on lakeshores, 31 of 149 (21%) in riparian strips, and 41 of 149 (28%) were captured in lichen tundra. Subadult females and males showed similar, but not as marked, preferences for the same habitats as the same sex adults. Twenty-five percent (47 of 186) of female subadults were captured in lichen tundra, 25 of 186 (13%) on lakeshores, and 24 of 186 (13%) on beach ridges. Twenty-one percent (41 of 196) of male subadults were captured on beach ridges, 31 of 196 (16%) on lakeshores, and 26 of 196 (13%) in willows.

The correspondence analysis of the data in Table 1 provides a multi-dimensional representation of the dependency between habitats and age and sex classes. Of this dependency, 90.2% is accounted for by only 2 axes (axis 1: 70.1%, axis 2: 20.1%). Plotting the coordinate figure scores for each habitat and age–sex category (from the correspondence analysis) on these 2 axes (Fig. 1) portrays the dependent relationships or similarities between habitat and age and sex classes.

The greatest degree of segregation of age and sex classes was between adult males and adult females of all categories (Fig. 1). Otherwise, associations of bears of each age and sex class are similar to those discussed above (Table 1). When judging the relative closeness of points, it is the horizontal or vertical distance between them that is important, not oblique distances. In particular, the observed pattern resulted from the strong association between adult males with coastal habitat types, while adult females were most strongly associated with inland habitats, primarily riparian and lichen tundra. Subadult females were close to the point of origin suggesting that, overall, they were found at expected levels throughout

Table 1. Number of polar bears of each age and sex class captured in each habitat type in the Hudson Bay Lowlands, Manitoba, from 15 August to 15 October, 1966–94.

Habitat	Male adult	Male subadult	Female adult alone	Female adult with COY	Female adult with yearling	Female subadult	Total
Lichen tundra	7	22	33	59	41	47	209
Coastal tundra	8	21	1	4	0	10	44
Beach ridge	79	41	7	5	11	24	167
Tidal flats	8	14	1	4	1	15	43
Willow	25	26	3	9	4	15	82
Wetland	3	9	9	13	4	11	49
Hummock	11	9	9	15	7	8	59
Spruce forest	5	7	9	13	10	9	53
Burn	0	1	0	1	0	2	4
Riparian	13	11	63	40	31	16	174
Lakeshore	39	31	57	37	38	25	227
Unclassified	2	4	8	0	2	4	20
Total	200	196	200	200	149	186	1131

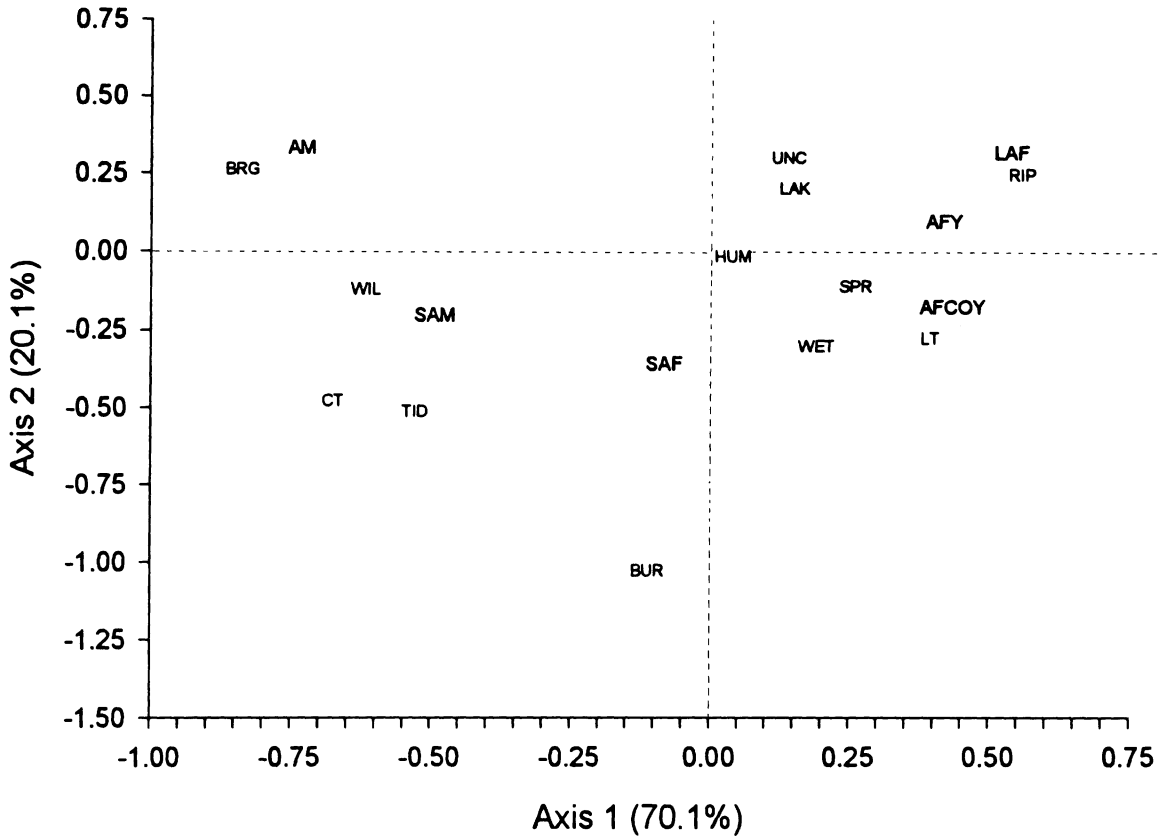

Fig. 1. Row and column profile plot from correspondence analysis of similarities among habitats and age and sex classes of polar bears in the western Hudson Bay Lowlands from 15 August to 15 October, 1966–94. (AM = adult male, SAM = subadult male, LAF = lone adult female, AFCOY = adult female with cubs-of-the-year, AFY = adult female with yearlings, SAF = subadult female, LT = lichen tundra, CT = coastal tundra, BRG = beach ridge, TID = tidal flat, WIL = willow, WET = wetland, HUM = hummock; SRP = spruce forest, BUR = burn, RIP = riparian, LAK = lakeshore, and UNC = unclassified.

all habitats. Subadult males were plotted well away from the point of origin toward adult males, though not as strongly. Apparently adult and subadult males have similar habitat preferences.

DISCUSSION

The distribution of bears of different age and sex classes appeared to be independent of proportional availability of different habitats. For example, coastal tundra is considerably more abundant than beach ridges, but far more bears of all ages and sex classes, especially adult males, were captured on beach ridges. In the inland areas, 2 of the most abundant habitats available, wetland and spruce forest, had very few bears. In contrast, the small, dry hummocks scattered through the extensive wetland areas comprised a relatively small total area but were used by similar numbers of bears of all age and sex classes than either the much more extensive spruce forests or wetlands.

The high proportion of bears found on lichen tundra, especially adult females with and without dependent young, may be misleading. Most areas of lakeshore and riparian habitats, both highly selected for by all groups of adult females, bordered on expanses of lichen tundra. Almost all bears first sighted on lichen tundra were along the edge, rather than in the open expanse. Thus, the apparent preference of polar bears for lichen tundra is more likely a consequence of the habitat it borders rather than a preference for the lichen tundra itself.

Adult Males

Adult males are approximately double the mass of adult females, so movement is more energetically expensive for them. Similarly, thermoregulation during warm or hot weather in summer or early fall may be energetically expensive if they cannot find habitat which is naturally cool. Therefore, if the principal objective for a bear coming ashore at break-up is to rest, minimize expenditure of

energy, and not overheat while it waits for freeze-up, one would predict that at least the most dominant age and sex class would be found in whatever habitats most efficiently meet that objective. Largely because of their size, but also because adult males occasionally kill bears of other age and sex classes (Taylor et al. 1985), adult males are the most dominant age and sex class, and all others normally defer to or avoid them (Stirling 1974, Latour 1981).

Adult males showed strong selection for coastal habitat types. These habitats require the least amount of travel to reach, and bears could remain cool there in the hot weather because of onshore winds and direct access to water if necessary. In coastal areas, adult males spend 70–90% of their time inactive, presumably to conserve their fat reserves while waiting for freeze-up in November (Latour 1981, Lunn and Stirling 1985), and feed little (Russell 1975, Knudsen 1978, Derocher et al. 1993). Although some adult males move inland in September and October when the weather cools, their average distances from the coast in those months were only 8 and 5 km, respectively (Derocher and Stirling 1990*a*). In comparison, family groups and lone adult females travelled an average of between 24 and 41 km inland, respectively, through the same period. Of adult males found inland, 3 times more were found on lakeshores than on riparian habitat (39 of 200 vs. 13 of 200 captures, respectively), possibly because lakeshores, like coastlines, offer greater exposure to wind for remaining cool in the warmer weather.

While on the coast during the fall, the testosterone levels of adult males reach their lowest concentrations for the year (Palmer et al. 1988). Probably because of lower hormone levels and the absence of critical resources such as food or breeding females to compete over, adult males generally tolerate each other and may reach relatively high densities along the beach ridges. Males often gather in groups of 4–6 individuals but as many as 14 have been reported (Derocher and Stirling 1990*b*). On the west side of the beach ridges, there are extensive areas of willows into which the bears retreat for cover later in the fall to escape cold winds and storms. This would account for a large proportion of the preference shown for willows by adult and subadult males. Lone adult females and females accompanied by cubs were found in willows less than predicted, possibly because of the presence of adult males, restricted visibility, and the potential risk of predation.

Subadult Males

Subadult male bears selected similar habitat to adult males, especially coastal tundra and beach ridges, although behavioral observations show they actively avoid adult males in the same areas (Latour 1981). Like adult males, they were found about 3 times more often on lake edges than in riparian habitat.

Lone Adult Females

Lone adult females exhibited a strong preference for riparian and lakeshore habitat in the inland areas, further from the coast than bears of all other age and sex classes (Derocher and Stirling 1990*a*). By doing so, they appear able to minimize interactions with other bears, especially adult males, while seeking sites for maternity dens. They dig and occupy dens in the frozen peat, mainly along the banks of streams and the edges of lakes, explaining their strong preference for these habitats. Although the precise timing is not known, pregnant females appear to occupy dens shortly after reaching the inland areas. Once in or near the entrances to their dens, they are able to rest within their thermoneutral range, avoid insects, and eventually give birth to their young in safety. Considering that these females must fast for approximately 8 months while producing and nursing young (Ramsay and Stirling 1988), it is probably imperative they expend minimal energy on anything other than maintenance and production of young.

In most years, <10% of the adult females are not pregnant in the fall (Derocher et al. 1992) but, unlike pregnant females, tend to remain near the coast in similar habitat to males, while actively avoiding them (Latour 1981, Derocher and Stirling 1990*a*). Nevertheless, the proportion of lone females that was not pregnant is too small to influence the overall pattern.

Adult Females with Dependent Cubs (COY and yearling)

Although we analyzed females accompanied by COY and those with yearlings independently, the results were so similar that we considered them together as adult females with dependent young. Two features stand out: their avoidance of coastal habitat types and their strong preference for riparian and lakeshore habitat inland. Few family groups were found in spruce forest or wetlands, even though both habitats are widespread in the inland areas, suggesting these areas are largely avoided.

Several factors could influence their preference for inland areas and habitats, which do not need to be mutually exclusive. Females with young actively avoid adult males on the sea ice (Stirling et al. 1993), probably in part because of the threat of predation (Taylor et al. 1985), but also because males sometimes take their kills away (Stirling 1974). However, since bears on shore

feed little, the inland distribution of females on land is more likely related to fear of male predation than to avoiding possible competition for food (Derocher and Stirling 1990*a*). Although there are relatively few observations of female or young polar bears killed by adult males on land during the ice-free period, some cases have been documented (Jonkel 1970, Lunn and Stenhouse 1985, Stirling unpubl. data), indicating that the threat of predation is real.

Although polar bears on land in western Hudson Bay appear to feed little (Russell 1975, Lunn and Stirling 1985, Ramsay and Hobson 1991), Derocher et al. (1993) reported that 34% of females and 26% of males (mostly subadults) in the inland areas showed evidence of feeding on berries. However, the extent of such feeding on berries and its nutritional importance is unknown. Berry-producing habitats such as lichen tundra, lakeshores, and riparian strips are occupied by females with dependent young. However, family groups go there before berries become available and remain there through most of the ice-free period, regardless of the relative strength of the berry crop. This suggests that berry feeding is less of a priority overall than other factors and is likely not the most important reason for selecting riparian or lakeshore habitat.

In years that berries were present, the cost of feeding relative to searching for berries might be low enough to make the activity worthwhile. Although such feeding is not felt to be significant in the overall diet (Lunn and Stirling 1985, Ramsay and Hobson 1991), it might assist bears to conserve their fat reserves. This could be beneficial if it permitted bears to lactate longer or allowed them to return to the ice in better condition, and would be critical for animals which came ashore with insufficient reserves to fast until freeze-up. The weight of bears coming ashore has varied among years. Derocher et al. (1993) documented an increase in the incidence of terrestrial feeding from 1987 through 1991; during the same period, body weights of adult female bears coming ashore decreased significantly (Derocher and Stirling 1992). This suggests that in years when bears come ashore in poorer condition or must spend more time ashore because of the timing of break-up or ice formation, supplemental food might become more important. Adult males on shore fed on vegetation significantly less frequently than did bears of other age and sex classes, contrary to what might be expected from comparisons to other bear species (e.g., Wielgus and Bunnell 1994).

The energetic cost of feeding on berries in the study area would be small relative to the cost of walking to the inland areas from the coast and back again, which most bears (except adult males) do anyway. Although we did not assess berry productivity quantitatively in the study area, in 1992 we searched for 1-m^2 sites in several localized areas where we thought densities of berries might be high enough to compare relative productivity between years. Even in these locations, we often searched >1 km^2 before finding a site worth sampling. Although our impression is subjective, we suggest that production of berries in the study area appeared to be much lower than in boreal or subalpine areas elsewhere in North America. Nevertheless, since the bears are already in the inland areas, the benefits of feeding on berries when they are available would not need to be large for feeding behavior to persist.

Finally, Derocher and Stirling (1990*a*) also suggested a possible secondary benefit to female offspring of travelling to the inland areas with their mothers in summer. Through this, subadult females may learn about the area to which they will eventually return to den as adults.

Thus, we suggest the primary reason females with dependent young go to the inland areas during the ice-free period is to avoid adult males. However, they may also take advantage of opportunities for supplemental feeding and female cubs may become familiar with their future denning area.

Subadult females

Subadult females are more widely distributed among inland habitats than adult males, but their overall preferences and avoidances parallel those of adult females. Like non-pregnant adult females, subadults did not avoid coastal habitats, although Latour (1981) found that subadult females tended to separate themselves from both subadult and adult males in an area where both were abundant. The association of subadult females with riparian and lakeshore habitats was lower than predicted, but their presence in adjacent lichen tundra areas was much higher. Derocher and Stirling (1990*a*) suggested that subadults may not regard adult males as a threat on shore, since visibility is great and competition for resources apparently nonexistent. Stirling (1974) suggested that yearling cubs and subadults can outrun adult males and may not be at risk from them. Thus, the apparent selection by subadult females for open areas such as beach ridges and lichen tundra may be partly because the greater visibility would make it easier to detect possible threats from other bears.

Bears of all age and sex classes were found in similar proportions on small hummocks (Table 1). A high (though unquantified) proportion of unoccupied hum-

mocks observed from the helicopter had old pits, and sometimes dens, if the hummocks were sufficiently large and vegetated. We suspect that the relatively isolated nature of these microsites makes them attractive to bears of all age and sex classes seeking a resting place where they are less likely to be disturbed, have good visibility of surrounding areas, and are exposed to cooling by breezes in warm weather because of being elevated above the surrounding landscape.

These results suggest that different age and sex classes of polar bears actively select specific habitat types in both coastal and inland areas of the Hudson Bay Lowlands during the ice-free period in Hudson Bay. Their choices are influenced by a variety of social and energetic factors, the signficance of which varies with different age and sex classes.

LITERATURE CITED

CLARK, D. 1996. Terrestrial habitat selection by polar bears (*Ursus maritimus*) in the western Hudson Bay Lowlands. M.Sc. Thesis, Univ. Alberta, Edmonton, Can. 119pp.

DEROCHER, A.E., D. ANDRIASHEK, AND I. STIRLING. 1993. Terrestrial foraging by polar bears during the ice-free period in western Hudson Bay. Arctic 46:251–254.

———, AND I. STIRLING. 1990*a*. Distribution of polar bears (*Ursus maritimus*) during the ice-free period in western Hudson Bay. Can. J. Zool. 68:1395–1403.

———, AND ———. 1990*b*. Observations of aggregating behaviour in adult male polar bears (*Ursus maritimus*). Can. J. Zool. 68:1390–1394.

———, AND ———. 1992. The population dynamics of polar bears in western Hudson Bay. Pages 1150–1159 *in* D.R. McCullough and R.H. Barrett, eds. Wildlife 2001: Populations. Elsevier Appl. Sci., London, U.K.

———, ———, AND D. ANDRIASHEK. 1992. Pregnancy rates and serum progesterone levels of polar bears in western Hudson Bay. Can. J. Zool. 70:561–566.

DIXON, W.J., EDITOR. 1992. BMDP statistical software manual. Version 7. Volume 2. Univ. California Press. 1,500pp.

DREDGE, L.A., AND F.M. NIXON. 1992. Glacial and environmental geology of northeastern Manitoba. Geol. Surv. Can. Memoir 432. Ottawa, Can. 80pp.

JONKEL, C. 1970. Behavior of captured North American bears (with comments on bear management and research). BioScience 20:1145–1147.

———, G.B. KOLENOSKY, R.J. ROBERTSON, AND R.H. RUSSELL. 1972. Further notes on polar bear denning habits. Int. Conf. Bear Res. and Manage. 2:142–158.

KERSHAW, K.A. 1974. Studies on lichen-dominated systems. X. The sedge meadows of the coast raised beaches. Can. J. Bot. 52:1947–1972.

———. 1977. Studies on lichen-dominated systems. XX. An examination of some aspects of the northern boreal lichen woodlands in Canada. Can. J. Bot. 55:393–410.

KNUDSEN, B. 1978. Time budgets of polar bears (*Ursus maritimus*) on North Twin Island, James Bay, during summer. Can. J. Zool. 56:1627–1628.

LATOUR, P.B. 1981. Spatial relationships and behaviour of polar bears (*Ursus maritimus* Phipps) concentrated on land during the ice-free season of Hudson Bay. Can. J. Zool. 59:1763–1774.

LUNN, N.J. 1986. Observations of non-aggressive behavior between polar bear family groups. Can. J. Zool. 64:2035–

———, AND G.B. STENHOUSE. 1985. An observation of possible cannibalism by polar bears (*Ursus maritimus*). Can. J. Zool. 63:1516–1517.

———, AND I. STIRLING. 1985. The significance of supplemental food to polar bears during the ice-free period of Hudson Bay. Can. J. Zool. 63:2291–2297.

PALMER, S.S., R.A. NELSON, M.A. RAMSAY, I. STIRLING, AND J.M. BAHR. 1988. Annual changes in serum sex steroids in male and female black (*Ursus americanus*) and polar (*Ursus maritimus*) bears. Biol. Reprod. 38:1044–1050.

PIERCE, W.G., AND K.A. KERSHAW. 1976. Studies on lichen-dominated systems. XLII. The colonization of young raised beaches in NW Ontario. Can. J. Bot. 54:1672–1683.

RAMSAY, M.A., AND K.A. HOBSON. 1991. Polar bears make little use of terrestrial food webs: Evidence from stable-carbon isotope analysis. Oecologia 86:598–600.

———, AND I. STIRLING. 1988. Reproductive biology and ecology of female polar bears (*Ursus maritimus*). J. Zool. (Lond.) 214:601–634.

RITCHIE, J.C. 1962. A geobotanical survey of northern Manitoba. Tech. Pap. Arctic Inst. North Am. 9. 48pp.

RUSSELL, R.H. 1975. The food habits of polar bears of James Bay and southwest Hudson Bay in summer and autumn. Arctic 28:117–129.

SHELFORD, V.E., AND A.C. TWOMEY. 1941. Tundra animal communities in the vicinity of Churchill, Manitoba. Ecology 22:47–69.

SJÖRS, H. 1959. Bogs and fens in the Hudson Bay Lowlands. Arctic 12:2–19.

STIRLING, I. 1974. Midsummer observations on the behavior of wild polar bears (*Ursus maritimus*). Can. J. Zool. 52:1191–1198.

———, D. ANDRIASHEK, AND W. CALVERT. 1993. Habitat preferences of polar bears in the western Canadian Arctic in late winter and spring. Polar Rec. 29:13–24.

———, C. JONKEL, P. SMITH, R. ROBERTSON, AND D. CROSS. 1977. The ecology of the polar bear (*Ursus maritimus*) along the western coast of Hudson Bay. Can. Wildl. Serv. Occas. Pap. 33. 64pp.

———, C. SPENCER, AND D. ANDRIASHEK. 1989. Immobilization of polar bears (*Ursus maritimus*) with Telazol® in the Canadian Arctic. J. Wildl. Dis. 25:159–168.

TAYLOR, M., T. LARSEN, AND R.E. SCHWEINSBURG. 1985. Observations of intraspecific aggression and cannibalism in polar bears (*Ursus maritimus*). Arctic 38:303–309.

WIELGUS, R.B., AND F.L. BUNNELL. 1994. Sexual segregation and female grizzly bear avoidance of males. J. Wildl. Manage. 58:405–413.

ZOLTAI, S.C., AND C. TARNOCAI. 1975. Perenially frozen peatlands in the Western Arctic and Subarctic of Canada. Can. J. Earth Sci. 12:28–43.

———, ———, G.F. MILLS, AND H. VELDHUIS. 1988. Wetlands of subarctic Canada. Pages 57–96 *in* Canadian Committee on Ecological Land Classification, ed. Wetlands of Canada. Nat. Wetlands Working Group, Polyscience Publ., Inc., Morin Heights, Que.